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ARTICLE

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Abstract
    Red Snapper *Lutjanus campechanus* is the most economically important reef fish in the Gulf of Mexico, and despite being intensively managed, the stock remains overfished. These fish are susceptible to pressure-related injuries (i.e., barotrauma) during fishing that compromise survival after catch and release. Barotrauma-afflicted fish may not only experience immediate mortality but also delayed mortality after returning to depth. This variability and unknown fate leads to uncertainty in stock assessment models and rebuilding plans. To generate better estimates of immediate and delayed mortality and postrelease behavior, Red Snapper were tagged with ultrasonic acoustic transmitters fitted with acceleration and depth sensors. Unique behavior profiles were generated for each fish using these sensor data that allowed the classification of survival and delayed mortality events. Using this information, we compared the survival of Red Snapper released using venting, nonventing, and descending treatments over three seasons and two depths. Red Snapper survival was highest at cooler temperatures and shallower depths. Fish released using venting and descender tools had similar survival, and both these groups of fish had higher survival than nonvented surface-released fish. Overall, Red Snapper had 72% survival, 15% immediate mortality, and 13% delayed mortality, and all fish suffering from delayed mortality perished within a 72-h period after release. Results from these field studies enhance the understanding of the delayed mortality and postrelease fate of Red Snapper regulatory discards. Moreover, these data support the practice of using venting or descender devices to increase the survival of discarded Red Snapper in the recreational fishery and show that acoustic telemetry can be a valuable tool in estimating delayed mortality.

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The success of catch-and-release fishing as a management tool is predicated upon the assumption that discarded fish will survive (Bartholomew and Bohnsack 2005; Cooke and Suski 2005; Arlinghaus et al. 2007). Many offshore reef fish species in deepwater environments routinely experience barotrauma when brought rapidly to the surface during fishing and, consequently, suffer an increased risk of discard mortality in catch-and-release fisheries (Rummer 2007). Certainly, the development of techniques that avoid or minimize injury or mortality associated with barotrauma has the potential to improve the management and recovery timelines for many reef fish species.

Gulf of Mexico Red Snapper *Lutjanus campechanus* is an ideal model species on which to test methods to reduce barotrauma-related injuries. This species commonly experiences severe barotrauma (Rummer and Bennett 2005), and a large proportion of the total catch may be discarded (Dorf 2003; Campbell et al. 2013). Red Snapper is considered the most economically important reef fish species in the Gulf of Mexico and has been heavily managed since the fishery was first classified as overfished in 1988 (Goodyear 1988; Hood et al. 2007). Management strategies enacted by the Gulf of Mexico Fishery Management Council (GMFMC) for the recreational fishery have included reducing bag limits, shortening fishing seasons, and setting minimum size limits with the goal of reducing fishing pressure and allowing stocks to rebound (see Hood et al. 2007 for comprehensive fishery management history). However, with the stock not yet fully rebuilt and almost two decades remaining in the rebuilding phase, management strategies have become increasingly strict and more controversial (Cowan et al. 2010). An unintended consequence of these tightened regulations has been an increase in the frequency of "regulatory discards" —fish that are required by law to be released because they do not meet size, season, or bag requirements.

Minimizing death after release is a common aim for fishery managers. One management strategy enacted by the GMFMC to increase survival in reef fish was a requirement to vent the swim bladder prior to release (GMFMC 2007). More recently, there has been some skepticism over the efficacy of venting in reducing discard mortality (Wilde 2009; Scyphers et al. 2013; Campbell et al. 2014), and studies specific to Red Snapper have shown positive (Gitschlag and Renaud 1994), neutral (Render and Wilson 1994, 1996), and negative (Burns et al. 2002) effects of venting on survival. An alternative to venting, and potentially a more effective release method, is rapid recompression using descender devices. This technique involves rapidly descending the fish back to depth on a weighted line prior to release to rapidly recompress the swim bladder and alleviate any barotrauma symptoms without having to vent the fish. Additionally, this method also avoids releasing the fish at the surface, where increased risk of predation exists (Burns et al. 2004). The venting regulation has since been rescinded (GMFMC 2013), which allows for the use of descender devices; however, the efficacy of these devices in reducing discard mortality in the Gulf of Mexico Red Snapper fishery warrants further research.

The results of studies quantifying discard mortality in the Gulf of Mexico recreational Red Snapper fishery remain highly variable—the latest estimate of discard mortality from a meta-analysis of studies ranges from 0% to 91% (Campbell et al. 2013). This large variability is influenced by multiple factors, including season, fishery sector, geographical region, and water depth, and is further convoluted by interactions among these factors (Gingerich et al. 2007). Moreover, the majority of these studies have only assessed immediate discard mortality, or mortality that is observed from surface observations within several seconds postrelease, while delayed mortality is unknown. Although Red Snapper that are capable of resubmerging unassisted after catch and release are presumed to survive, this assumption is largely untested, and there is evidence that the ability to swim away is unrelated to survival (Bettoli and Osborne 1998; St John and Syers 2005; Diamond and Campbell 2009). A substantial proportion of fish may undergo delayed mortality hours to several days after a supposed successful release (Rummer and Bennett 2005). Studies attempting to estimate delayed mortality have used field caging experiments (Gitschlag and Renaud 1994; Render and Wilson 1994; Diamond and Campbell 2009; Roach et al. 2011) or in-laboratory hyperbaric chamber simulations (Rummer and Bennett 2005; Burns 2009; Drumhiller et al. 2014). While considerable success has been achieved using these methods, these study designs do not allow for tracking postrelease survival over longer time periods and they have an inherent bias because they exclude predatory effects, prevent foraging, and restrict natural movement (Campbell et al. 2013).

One method to alleviate the artifact biases associated with estimating delayed mortality using passive tagging or cage studies is through the use of ultrasonic acoustic telemetry (Campbell et al. 2014). This technique has already been extremely successful tracking the movements, long-term residency, and site fidelity of Red Snapper (Szedlmayer and Schroepfer 2005; Peabody and Wilson 2006; Westmeyer et al. 2007; Topping and Szedlmayer 2011a) but has not yet been used to quantify discard mortality in the recreational fishery. Transmitters equipped with accelerometer and depth sensors allow researchers to monitor the postrelease survival and behavior of fish. For fish experiencing barotrauma, these tags can provide information on presence or absence, mortality (no acceleration), postrelease depth preference, and activity level compared with fish not experiencing barotrauma. There have been no published tagging studies that used these advanced acoustic tags to examine the physiological responses of Red Snapper, particularly as they relate to regulatory discards and examining delayed mortality. Using this tagging methodology not only allows us to avoid cage artifacts but also to replicate postrelease fishing practices most reflective of the actual fishery and approximate the most natural behavioral characteristics of the fish.

The primary goal of this study was to quantify the extent of immediate and delayed mortality due to barotrauma impairment in the Red Snapper recreational fishery using surface observations and acoustic telemetry. Specifically, we tested (1) whether certain release treatments are more favorable for increasing survival after catch and release and if using descender devices or venting tools are a better alternative to not venting, (2) whether the season of capture associated with differences in water temperatures and the presence of thermoclines influences survival, and (3) if the depth of capture influences survival. This study will help managers better understand how delayed mortality may factor into overall discard mortality estimates and determine which release strategies maximize the chances of survival for Red Snapper discarded by recreational anglers.

METHODS

Release treatments.—Four standing oil and gas platforms approximately 50 km east of Port Aransas, Texas, were selected as study sites for these experiments (Figure 1). Sites MU-762-A and MU-759-A (approximately 27°45′N,

96°35′W) reside at a water depth of 50 m and sites MI-685-B and MI-685-C (approximately 27°55′N, 96°35′W) at a water depth of 30 m. Prior to sampling, fish were randomly assigned to one of four release treatments: (1) vented surface release, (2) nonvented surface release, (3) descended bottom release, and (4) control (no barotrauma). Surface-released fish were released into an open-bottom 1.0-m³ holding cage with mesh walls to protect fish from predation and enable retrieval of fish (and transmitters) that experienced immediate mortality at the surface. The number of immediate surface mortalities after catch and release was recorded for each trial and incorporated into the analyses. Vented surface-released fish were punctured in the abdomen posterior to the pectoral fin using a venting tool (Team Marine USA prevent fish venting tool), tagged, and released at the surface. Descended bottom-released fish were not vented prior to tagging but, instead of being released at the surface, were forced back to depth quickly using a weighted line with an inverted barbless hook (Shelton Fish Descender) attached to the fish's jaw. Once at the seafloor, fish were released with a slight upward pull of the line to release the hook from the jaw.
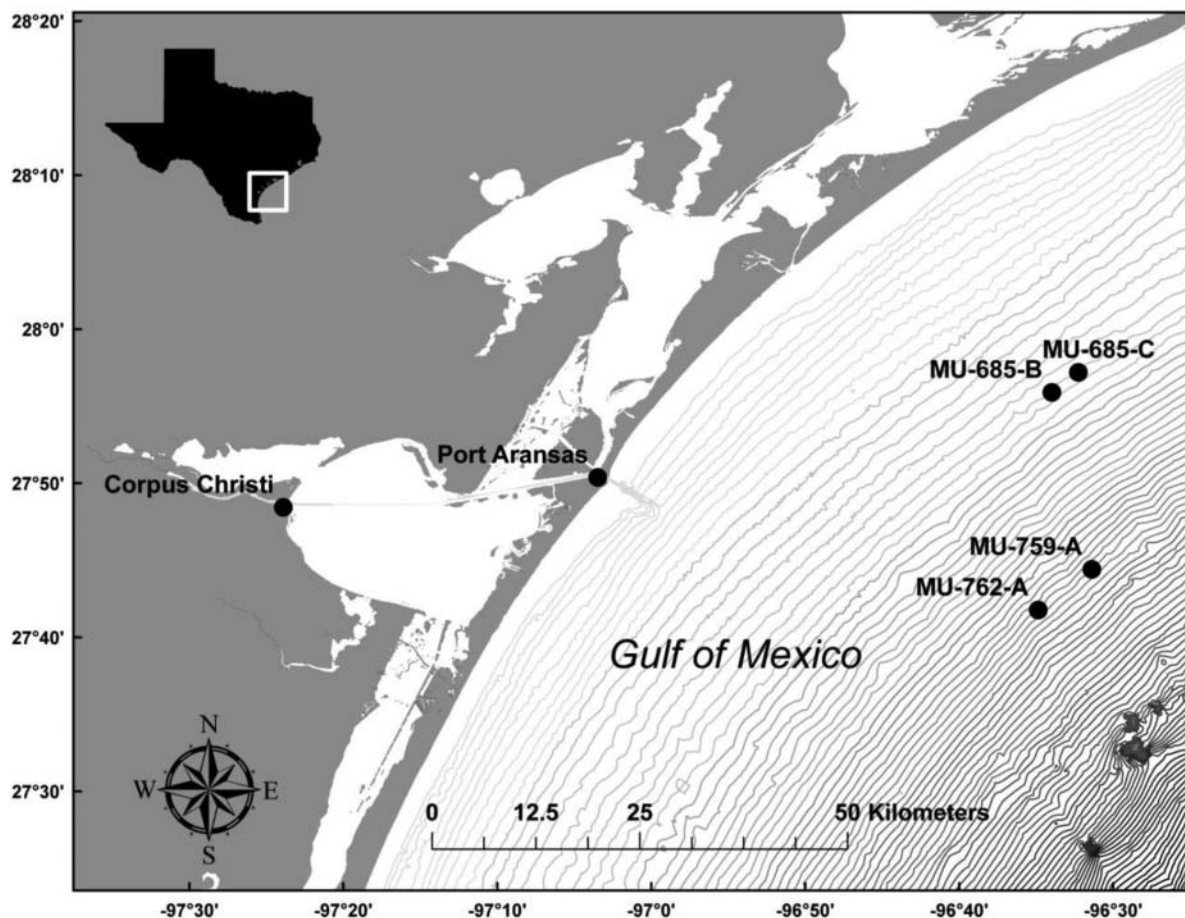

FIGURE 1. Study sites (standing oil and gas platforms) in the Gulf of Mexico off the southern Texas coast, where field tagging experiments occurred. Sites MU-685-B and MU-685-C reside at water depths of 30 m and sites MU-762-A and MU-759-A at 50 m.

Control fish showed no evidence of barotrauma prior to tagging and release. To achieve this, fish were captured using single hook and line at the 30-m platforms prior to experimental trials, transported to the Texas A&M AgriLife Research Mariculture Laboratory in Port Aransas, Texas, and held in 6.4-m³ tanks. Fish were treated for parasites using copper (II) sulfate and were fed three times weekly to satiation with a diet of squid *Loligo* sp. and sardines *Sardinella* sp. Fish recovered and began feeding quickly (typically within 24 h), and the condition and behavior of these fish were closely monitored. After a 3-week holding period, fish appeared healthy and acclimated to surface pressure, and it was assumed that any effects of barotrauma from capture had healed. Fish were then transported in oxygenated live wells to the study sites, where they were tagged and released along with the fish assigned to the other release treatments in randomized order.

Fish tagging.—Red Snapper were captured from the seafloor at each site by experienced anglers using a rod and reel equipped with 6/0 Lazer Sharp circle hooks baited with squid, scad *Trachurus* sp., or sardines. This gear type and bottom fishing strategy are the standard fishing practices used in the recreational Red Snapper fishery. Fish were measured for maximum total length (mm) and assessed (presence or absence) for six externally visible barotrauma symptoms: everted stomach, swollen and hard abdomen, exophthalmia (eyes forced from orbits), distended intestines, subcutaneous gas bubbles, and bleeding from the gills. A barotrauma impairment score (scale: 0–1) was calculated by summing the number of visible symptoms divided by six—the total number of possible symptoms (Diamond and Campbell 2009). All fish that were tagged had been captured by hooking in the mouth. Fish that appeared obviously moribund or deceased after capture were not tagged in order to eliminate the possibility of hook-induced mortality from our study. The focal point of this study was to examine only barotrauma effects on discard and delayed mortality; thus, we controlled for the effects of mortality from other causes, such as hook mortality, by purposefully selecting fish for which barotrauma was the only evident stressor. Significant differences in total length and barotrauma impairment among release treatments were tested using an analysis of variance (ANOVA; $\alpha = 0.05$).

Red Snapper were externally tagged with Vemco V9AP ultrasonic coded transmitters (V9AP-2H; 46×9 mm; 69 kHz; random delay interval: 30–90 s; estimated battery life: 45 d) containing built-in acceleration and pressure (i.e., depth) sensors. To measure acceleration, the V9AP tags calculate a value (m/s²) that represents the root mean square acceleration on three axes (*X*, *Y*, and *Z*) averaged over a fixed time interval:

$$m/s^2 = \sqrt{x^2 + y^2 + z^2} \text{ averaged over time (T).} \quad (1)$$

Depth was calculated by an algorithm that converts pressure sensors to a depth value (maximum depth = 100 m). Because one goal of our study was to explore survival under a variety of release treatments, fish were rapidly (<3 min)
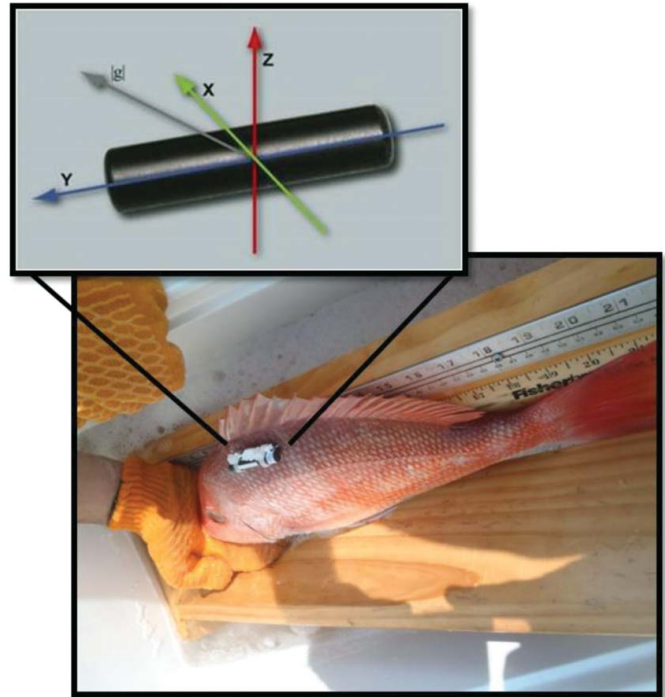

FIGURE 2. Acoustic transmitters were externally attached to prevent the unavoidable venting associated with internal tag implantation methods (lower panel). Vemco V9AP accelerometer tags measure the animal's acceleration signal (|g|) along three axes (*X*, *Y*, and *Z*) averaged over a fixed time interval (upper panel).

tagged externally without anesthesia to best replicate normal catch-and-release practices and minimize artifacts associated with tagging-related surgeries. One challenge was to prevent the unavoidable venting that is associated with the incision and suture procedures of traditional internal tag implantation; therefore, we developed and validated a protocol to attach tags to fish externally. Tags were positioned below the anterior dorsal spines approximately 2–3 cm below the dorsal edge, and fish were punctured between the 2nd and 3rd pterygiophores below the anterior dorsal spines using a sterile stainless steel hollow surgical needle. A plastic cinch-up external Floy tag was passed through one hollow needle, attached to the acoustic transmitter, and passed back through a second hollow needle between the 4th and 5th pterygiophores and secured so that the orientation of the transmitter was parallel to the fish and on the opposite side of the point of attachment (Figure 2). Fish were held in a tagging cradle with their gills submerged in oxygenated water to reduce potential injury or stress from emersion while still allowing the fish to ventilate during the tagging procedure. An externally visible dart tag containing identification and reward information was also inserted into the posterior dorsal spine region in the event that the fish were recaptured by anglers. During preliminary trials (*n* = 20), tag presence did not impair fish behavior and tag retention using our external attachment method was 100% for at least 20 d after the fish were released (Johnson et al. 2015).

Experimental design.—Three tagging trials occurred during winter 2010, summer 2010, and spring 2011. Winter and summer trials were performed at a water depth of 50 m on site MU-762-A. Twenty fish were tagged and released on site during each season using one of three release treatments: control, nonvented surface release, or descended bottom release. However, because of the repeated inability of nonvented fish to resubmerge during the summer trial, we added a vented surface release treatment. We subsequently included this treatment in our spring trial and incorporated a second depth into the experimental design to test for differences between capture depths of 30 and 50 m. Thirty-two fish were tagged at each depth, with all four release treatments included. Two Vemco VR2W-69kHz acoustic monitoring receivers were attached to platform crossbeams by scuba divers at each study site. Receivers were placed at depths of approximately 20 and 30 m for 50-m sites and at 15 and 25 m for 30-m sites. The detection range of VR2W receivers in this environment from previous studies conducted by our research group (authors' unpublished data) and other studies (Topping and Szedlmayer 2011a; Kessel et al. 2014) shows that after 500 m there is a substantial drop-off in detection efficiency. Therefore, we assumed a maximum detection range of 500 m for this study, which, combined with the known high site fidelity of Red Snapper (Szedlmayer and Schroepfer 2005; Westmeyer et al. 2007; Topping and Szedlmayer 2011a), ensured that we were able to detect tagged fish that remained on site for the duration of our experiment. During each sampling event, we measured water temperature, salinity, dissolved oxygen, and conductivity using a Manta2 water quality multiprobe (Eureka Environmental Engineering). Hourly sea surface temperatures for 10 d after tagging were obtained from the National Oceanic and Atmospheric Administration–National Data Buoy Center station 42020 ($26°58'$N, $96°42'$W). Significant differences in sea surface temperatures among seasons were tested using an ANOVA ($\alpha = 0.05$).

Fate classification.—The VR2W receivers were retrieved from the study sites after approximately 60 d, and data were uploaded to Vemco VUE software and exported for analysis to R version 3.0.2 (R Development Core Team 2013). Acceleration and depth profiles for each fish were plotted over time using tag sensor data. Using these unique acoustic profiles along with surface observations, the fate of each individual was classified into one of four categories: survival, surface mortality, delayed mortality, or unknown. Fish experiencing mortality at the surface were retrieved and transmitters reused. These surface mortalities did not yield an acoustic profile but were counted towards estimates of total overall mortality; therefore, mortality equaled the sum of immediate mortality witnessed by surface observations plus delayed mortality as indicated by acoustic returns. Fish that did not register sufficient detections (≤ 5 pings) were classified as unknown because it was not possible to classify these events as either survival or delayed mortality. These fish were omitted from

subsequent analyses, which reduced the sample size; however, we wanted to be certain the fate of the fish was accurately assigned. Fish classified as survivors exhibited active acoustic profiles with frequent bursts in acceleration and changes in depth. These included both resident fish that remained on site continuously for the duration of the tag life and fish that were determined to have emigrated from the array (Heupel and Simpfendorfer 2002). Emigrants showed similar active acceleration and depth profiles before sudden cessation of detections. Delayed mortality events were classified by initially active acceleration and depth movements followed by a sudden drop-off to zero acceleration and depth equal to the seafloor within 3 d.

Survival analysis.—Percent survival was calculated using the binomial distribution for two outcomes: survival and mortality. Survival estimates ($\hat{S}$) were calculated following equations in Pollock and Pine (2007):

$$\hat{S} = \frac{x}{n}, \tag{2}$$

with a standard error of

$$\text{SE}(\hat{S}) = \sqrt{\frac{\hat{S}(1 - \hat{S})}{n}}, \tag{3}$$

where x is the number of survivors and n is the total number of tagged fish minus the fish classified as unknown (i.e., $n =$ survivors + surface mortalities + delayed mortalities). Percent survival among release treatments at 50 m was compared among the three seasons, and the effect of capture depth at 30 m versus 50 m on the fate of discarded Red Snapper was compared during the spring.

The Cox proportional hazards model (Cox 1972), built into the "survival" package in R (Therneau and Grambsch 2000), was used to examine the relationship between survival and multiple explanatory variables (Sauls 2014). The Cox model is a semiparametric regression method for survival data. It provides an estimate of the treatment effect on survival after adjustment for other covariates in the model and gives an estimation of the hazard ratio (in this case the proportional risk of death) among levels within each of these explanatory variables. For survival analysis, this method is advantageous over logistic regression models because it can account for survival times and censored data, whereas regression models do not. Additionally, hazard ratios between covariates may be estimated without needing to specify the underlying baseline hazard, which may not be known. The Cox proportional hazards model is given by the following:

$$h(t) = h_0(t) \exp\left(\sum_{i=1}^{p} \beta_i X_i\right), \tag{4}$$

where $h_0(t)$ is an unspecified function representing the baseline hazard, β_i is the regression coefficients, and X_i is the explanatory variables or covariates in the model. A stepwise logistic regression using Akaike information criteria values was performed to determine which covariates to include in the Cox proportional hazards model.

RESULTS

Fish Tagging

A total of 111 Red Snapper ranging from 280 to 651 mm total length (mean $\pm$ SE = 446 $\pm$ 8 mm) were captured and tagged over three seasonal trials. No significant differences existed in total length among release treatments (ANOVA: $F_{3,\ 106} = 2.13$, $P = 0.10$). Fish released under vented, non-vented, and descended release treatments had a mean $\pm$ SE barotrauma impairment score of 0.32 ± 0.02 and were not significantly different (ANOVA: $F_{2,\ 89} = 0.41$, $P = 0.66$). All control treatment fish had a barotrauma impairment score of 0 at the time of release.

Temperature was plotted against depth using the observed hydrographic water data to determine if thermoclines in the water column were present and at what depths they occurred (Figure 3). Winter 2010 had a thoroughly mixed water column at a constant temperature of 24°C. Water temperatures from 22°C to 31°C occurred in the summer 2010 profile, with a steep thermocline observed beginning at 25 m and continuing to the seafloor. Spring 2011 had a temperature range of 3.5°C (23.5°C at the surface to 20.0°C at the seafloor), with a thermocline beginning at a depth of 20 m. Mean sea surface temperatures during the first 10 trial days for each season were significantly different (ANOVA: $F_{2,\ 716} = 5,102$, $P < 0.001$; Figure 4). Winter temperature was relatively constant over 10 d and averaged 23.0 ± 0.4°C (mean $\pm$ SD). Summer temperatures also remained constant for 10 d and averaged 30.5 ± 0.4°C. In the spring, temperature had a slight increasing trend over 10 d and averaged 25.0 ± 0.7°C.

Fate Classification

The classification fates from all trials are presented by season, depth, and release method (Table 1). In the spring season when multiple sites were included in the experimental design, there were no site-to-site differences; therefore, the two 30-m and two 50-m sites were each pooled together. Surface mortalities ($n = 13$) were immediate and were caused by the inability to resubmerge unassisted, typically because of overly positive buoyancy from gas expansion in the swim bladder in non-vented fish. Sixty-two fish survived and exhibited active acceleration and depth profiles. Survivors included both residents that remained on site continuously (Figure 5A) and emigrants that left the array (Figure 5B). There were 11 fish that experienced delayed mortality (Figure 5C), and 25 fish were
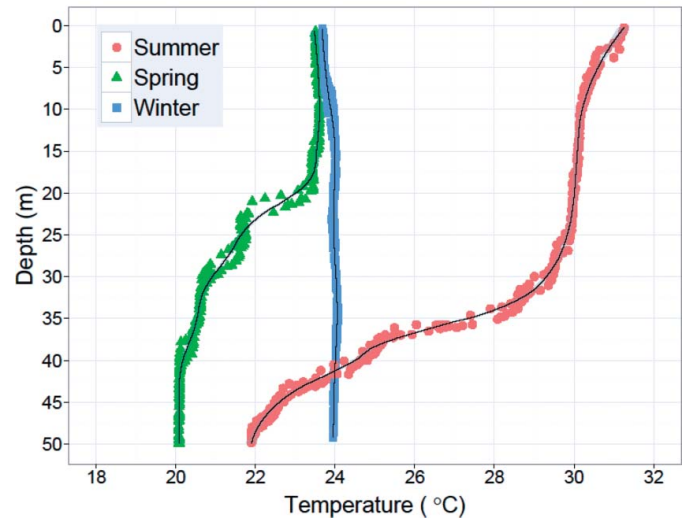

FIGURE 3. Temperature versus depth data collected on the day of tagging for each seasonal trial using a Manta2 water quality multiprobe at oil and gas platform site MU-762-A (water depth of 50 m). The black smoothing lines were fitted to the temperature data using a Loess model.

classified as fate unknown (Figure 5D). To examine the time elapsed to a delayed mortality event, the acceleration and depth acoustic profiles of all fish classified as suffering delayed mortality were plotted over time. By approximately the third day, all fish showed acceleration values of 0 and a depth equivalent to the bottom depth (Figure 6). After this time period
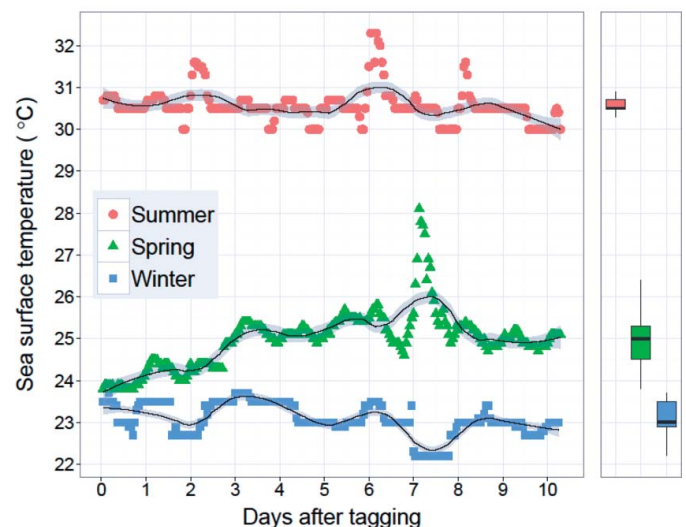

FIGURE 4. Sea surface temperatures during the first 10 d fish were at liberty for three seasonal tagging trials. The data was obtained from the National Oceanic and Atmospheric Administration–National Data Buoy Center buoy 42020 (26°58′N, 96°42′W). The boxplots show the distribution of temperature data for each season; the thick horizontal line in each box indicates the median, the box dimensions represent the 25th–75th percentiles, and the error bars represent the 10th and 90th percentiles. The black smoothing lines were fitted to the temperature data using a Loess model.

TABLE 1. Summary of the results of Red Snapper experimental trials. Tagged indicates the number of fish tagged and released, including those that perished on the surface, while fate unknown indicates fish whose fate was unclassifiable as a survivor or a mortality. Sample size (n) equals the number of fish tagged minus those whose fate was unknown. Surface mortality indicates fish that perished at the surface, and delayed mortality indicates fish that exhibited delayed mortality (perished in < 3 d). Survivor indicates fish that exhibited long-term (> 3-d) survival. The survival estimate ($\hat{S}$) is calculated from equation (2), with the standard error (SE) of the survival estimate calculated from equation (3). Note that "n/a" denotes that the vent treatment was not performed in the winter season.

Trial and total	Tagged	Fate unknown	n	Surface mortality	Delayed mortality	Survivor (x)	$\hat{S}$	SE ($\hat{S}$)
Winter – 50 m	22	4	18	2	2	14	0.78	0.10
Control	4	1	3	0	0	3	1.00	0.00
Descend	8	2	6	0	2	4	0.67	0.19
Nonvent	10	1	9	2	0	7	0.78	0.14
Vent	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Summer – 50 m	25	5	20	5	4	11	0.55	0.11
Control	3	0	3	0	1	2	0.67	0.27
Descend	9	3	6	0	1	5	0.83	0.15
Nonvent	8	1	7	4	2	1	0.14	0.13
Vent	5	1	4	1	0	3	0.75	0.22
Spring – 50 m	32	9	23	3	5	15	0.65	0.10
Control	6	4	2	0	0	2	1.00	0.00
Descend	8	2	6	0	2	4	0.67	0.19
Nonvent	10	0	10	3	1	6	0.60	0.15
Vent	8	3	5	0	2	3	0.60	0.22
Spring – 30 m	32	7	25	3	0	22	0.88	0.06
Control	6	3	3	0	0	3	1.00	0.00
Descend	7	0	7	0	0	7	1.00	0.00
Nonvent	10	2	8	2	0	6	0.75	0.15
Vent	9	2	7	1	0	6	0.86	0.13
Total	111	25	86	13	11	62	0.72	0.05

elapsed, there were no further delayed mortality events. All delayed mortality events occurred in trials at 50 m; there was no delayed mortality at 30 m.

Survival Analysis

Based on the classifications described from acoustic profiles, survival was compared among release treatments over all seasons and depths ($n = 86$). Survival was highest for control fish, followed in decreasing order by those with a descended bottom release, vented surface release, and nonvented surface release (Figure 7). All release treatments in winter and spring had similar survival; however, fish released nonvented during summer experienced much lower survival than those in vented or descended release treatments (Table 1; Figure 8). Between the two depths in spring, control fish experienced 100% survival, and survival was higher for every experimental release treatment at 30 m (Table 1). Immediate surface mortality was highest in the summer and lowest in the winter (Figure 9). Delayed mortality was higher in the summer and spring at 50 m than in the winter and did not occur in the spring at the 30-m depth. Overall, there was 72% survival, 15% surface

mortality, and 13% delayed mortality for all fish in this study (Table 1).

Stepwise logistic regression using Akaike information criteria values identified release method, season, depth, and total length as significant covariates to be used in the Cox proportional hazards model, and these covariates had a significant effect on survival (Log-rank test: $\chi^2 = 20.98$, df = 7, $P < 0.01$, $n = 86$). Based on the calculated hazards ratio, descended fish were 2.3 times, vented fish 3.7 times, and nonvented fish 6.9 times as likely to perish as control fish; nonvented fish were 3.0 times and 1.9 times more likely to perish than descended and vented fish, respectively; fish released in winter were 1.6 times and in summer 5.0 times as likely to perish as fish released in the spring; and fish released after capture from a 50-m depth were 2.5 times as likely to perish as fish caught at a 30-m depth (Table 2). Decreases in total length resulted in a slightly less risk of mortality; smaller fish had higher chances of survival than larger fish.

DISCUSSION

There has been considerable debate regarding the best release practices for increasing survival in catch-and-release
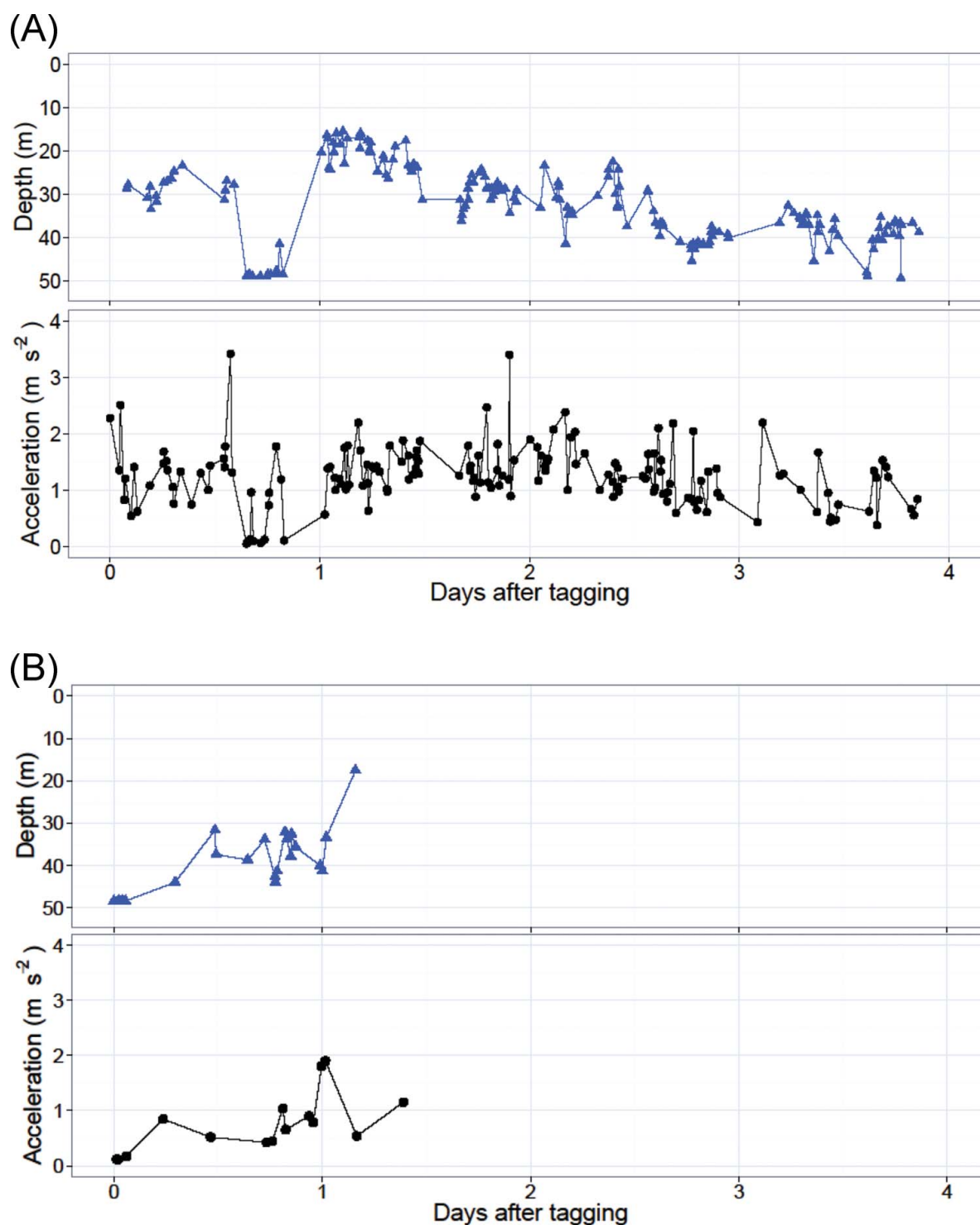
(A)

(B)

FIGURE 5.   Acoustic telemetry depth and acceleration profiles of tagged Red Snapper for 4 d following their catch and release. Each point represents individual acoustic detections, and they are connected by lines for visualization. Triangles represent the depth profile for each fish, and solid dots represent acceleration. **(A)** Resident survivors showed active acceleration and depth profiles and remained on site continuously, while **(B)** emigrant survivors exhibited active profiles similar to the resident survivors but left the array. **(C)** Delayed mortality profiles showed that before 3 d the fish had fallen to the seafloor and perished, showing no further vertical movement or acceleration, and **(D)** unknown profiles did not contain sufficient data to classify them as either survivor or delayed mortality.
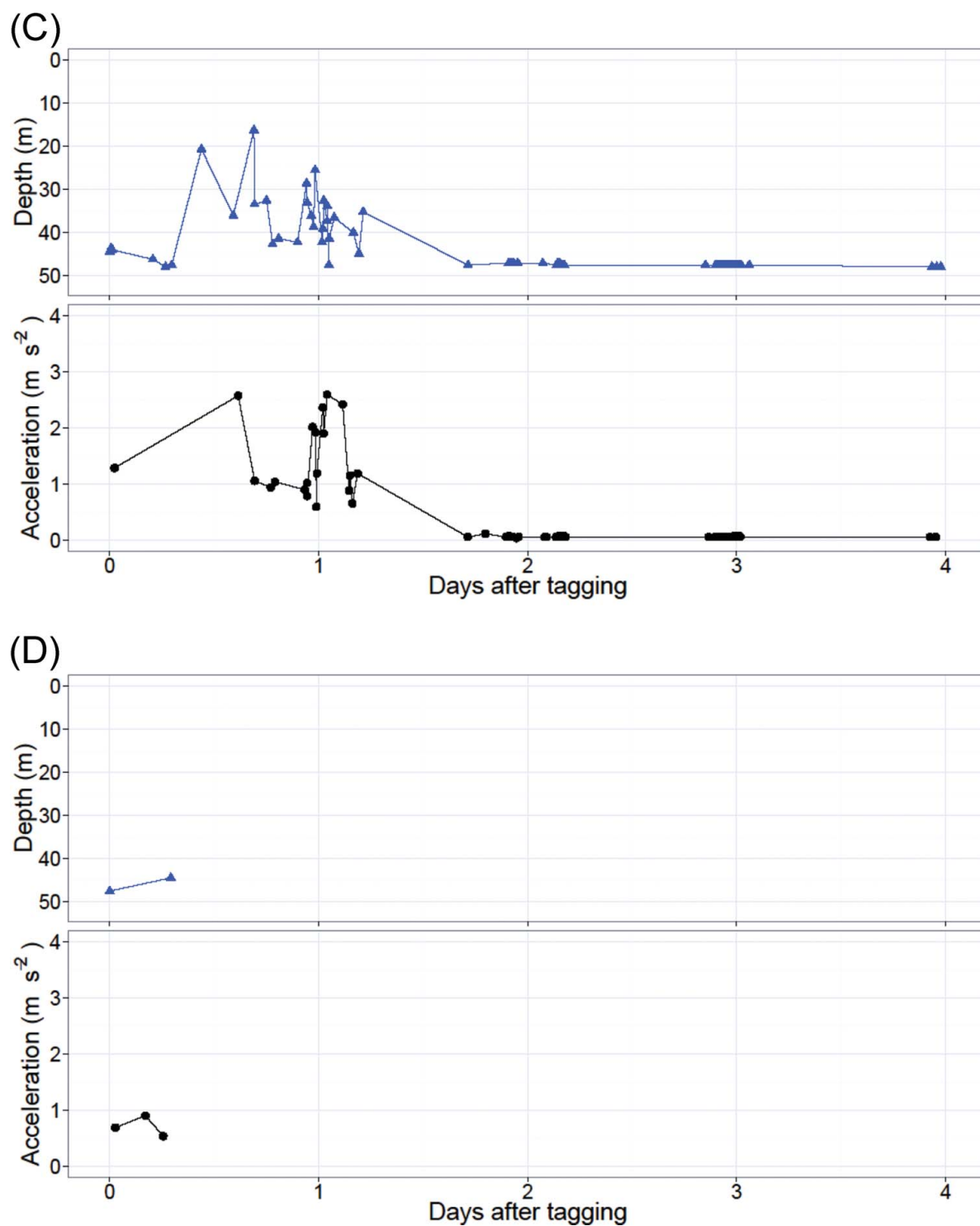
(C)

(D)

FIGURE 5. Continued.

fisheries, with differing results depending on species, season, depth of capture, angler experience, fish size, and a variety of other factors. For Red Snapper in the Gulf of Mexico, the question of venting or not venting has recently been at the forefront of this debate, with contradictory results among different studies (Wilde 2009) and confusion at the management and regulation level. This uncertainty has subsequently contributed to the GMFMC rescinding the requirement of venting prior to release after establishing this requirement only 5 years prior. Recently, highly
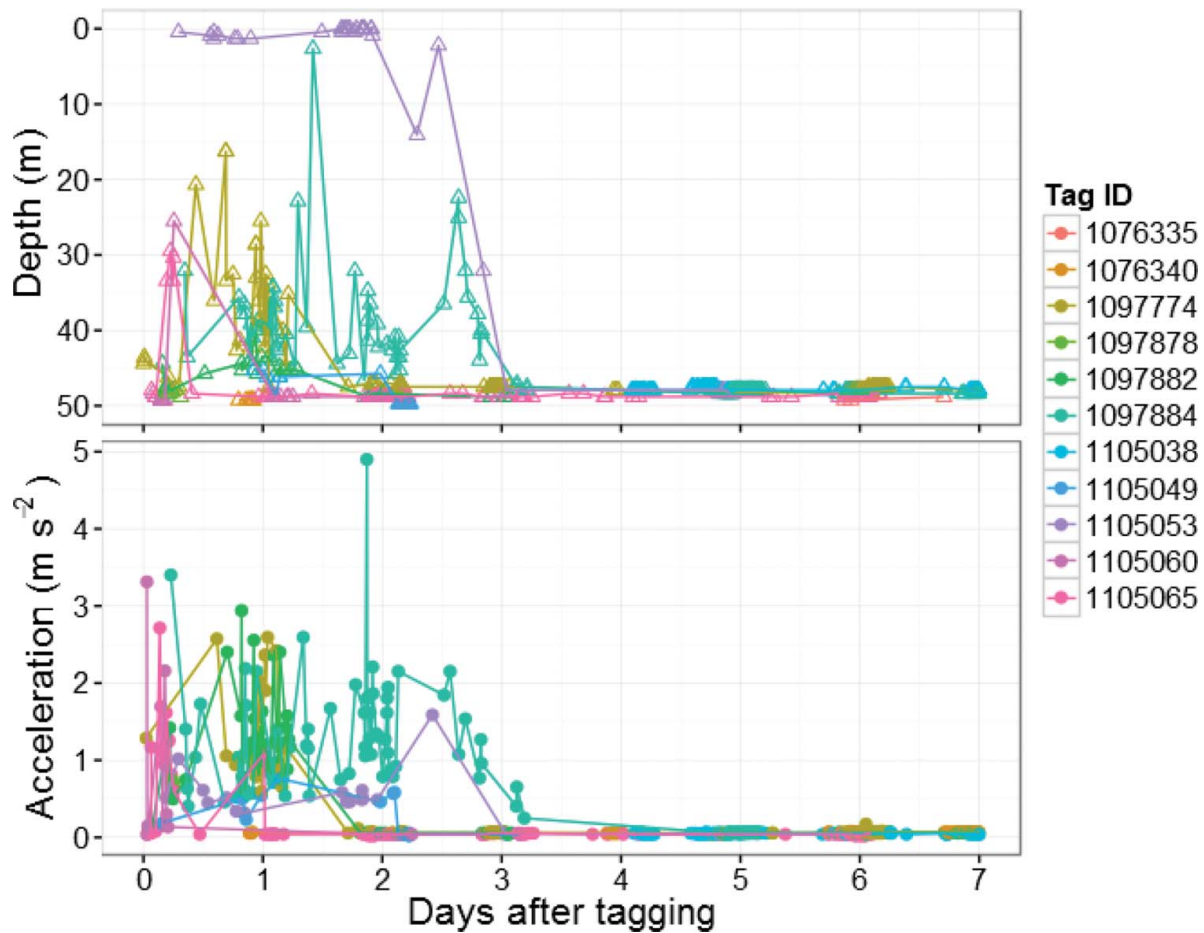
FIGURE 6. Acoustic telemetry depth and acceleration profiles of all acoustically tagged Red Snapper classified as delayed mortality for 1 week after catch and release ($n = 11$). The points represent individual acoustic detections and are connected by lines for visualization. The triangles in the upper panel represent depth; the solid dots in the lower panel represent acceleration. All delayed mortality events occurred in trials at a water depth of 50 m.
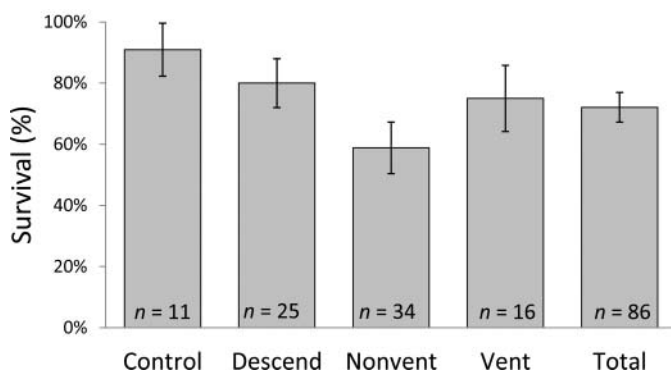

FIGURE 7. Percent survival (error bars indicate SE) of Red Snapper classified by acoustic profiles over all seasons and depths (summer, winter, spring–50 m, spring–30 m). Fish classified as fate "unknown" from acceleration and depth profiles are omitted in the analysis; therefore, sample size (n) for each group is equal to the number of fish tagged minus the unknowns. The four release treatments included the following: control fish (i.e., no barotrauma), descended release (Shelton fish descender), nonvented surface release, and vented surface release.

controlled laboratory experiments using hyperbaric chambers strongly advocated for venting in reducing discard mortality (Drumhiller et al. 2014); however, this study did not consider the impact of season (i.e., water temperature) on survival. The field observations here clearly showed survival was highly dependent upon season. While the majority of nonvented fish in our study survived catch and release during the winter and spring trials, only one fish survived in summer. Additionally, the largest number of immediate surface mortality events occurred in summer and the bulk of those mortalities were from fish that were unvented and released at the surface. Render and Wilson (1994) observed a similar interaction between season and release treatment. With the recreational fishing season occurring during the summer months (GMFMC 2015), the threat of immediate surface mortality is magnified by the number of anglers fishing for Red Snapper. Thus, using appropriate release methods to reduce the risk of mortality is imperative for increasing postrelease survival.
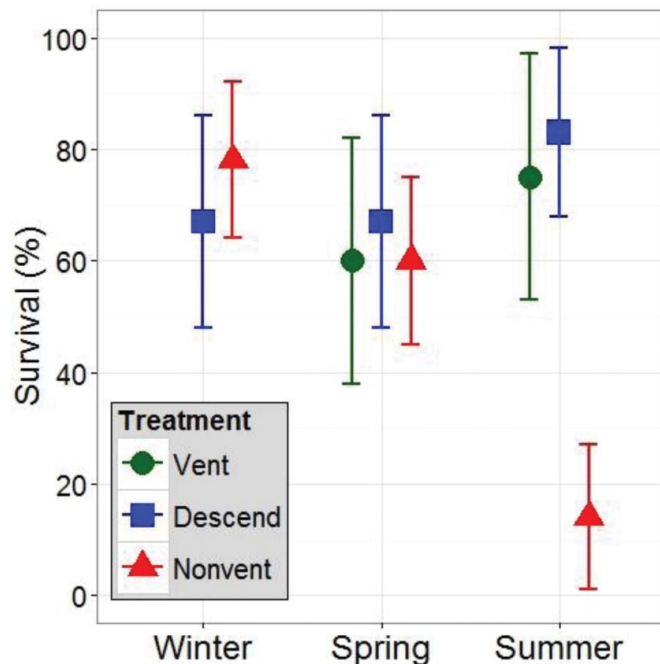
FIGURE 8. Percent survival (error bars indicate SE) of Red Snapper during field trials for three seasons: winter, spring (50-m sites only), and summer. Fish classified as fate "unknown" from acceleration and depth profiles are omitted in the analysis; therefore, the sample size (*n*) for each group is equal to the number of fish tagged minus the unknowns. The release treatments included the following: descended release (Shelton fish descender), nonvented surface release, and vented surface release. Note that the vented treatment was not performed in winter.

Temperature, Depth, and Release Treatments

Thermal stress occurs when captured fish are displaced and released in water temperatures that extend beyond their temperature tolerance range or in temperatures in which they are not acclimated (Cooke and Suski 2005; Gingerich et al. 2007; Diamond and Campbell 2009; Gale et al. 2013). Thermal stress caused by elevated water temperatures causes numerous
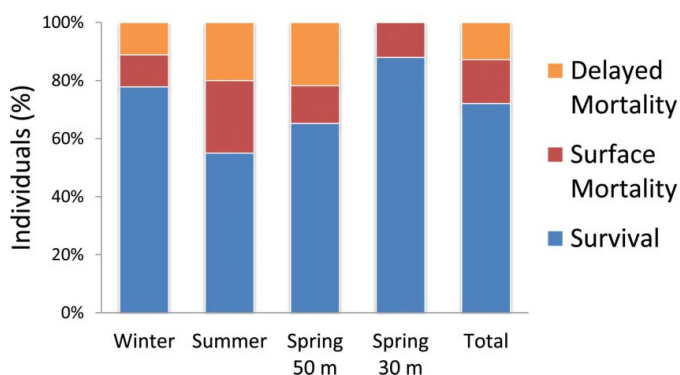

FIGURE 9. Stacked bar graph grouping all release treatments that shows the known fates of individuals by season based on acoustic profiles (survival, surface mortality, or delayed mortality). Each column is reported as a percentage out of 100%. Winter and summer trials were both performed at sites with a water depth of 50 m.

physiological and behavioral changes that can have profound effects on cellular function and metabolic activity (Fry 1971; Prosser 1991; Cooke and Suski 2005). Additionally, levels of dissolved oxygen are depressed at higher water temperatures and this may cause additional physiological problems in catch-and-release fisheries (Arlinghaus et al. 2007). High surface-to-bottom temperature differentials decreased survival in Black Rockfish *Sebastes melanops* (Hannah et al. 2012) and Red Snapper (Diamond and Campbell 2009). In our study, fish tagged and released in the summer season were five times as likely to perish as fish tagged in spring and two and a half times as likely as fish tagged in winter. The increased risk of mortality associated with higher sea surface temperatures during summer is likely exacerbated by large temperature differentials produced by the summer thermocline. Fish caught and released in the summer were brought from bottom temperatures of 22°C up to 31°C at the surface, a differential of 9°C. In contrast, spring fish experienced a much smaller 3.5°C differential and winter fish experienced < 1°C differential, and these fish had considerably higher survival rates. Summer sea surface temperatures approached the 33°C upper tolerance limit of Red Snapper (Moran 1988). Coupled with the additional physiological stress associated with a 9°C water temperature change (i.e., thermocline), these warmer surface waters in summer likely played a significant role in reducing Red Snapper survival after catch and release.

Rapid recompression strategies using descender devices showed positive benefits for Red Snapper in this study. These fish were three times as likely to survive as fish that were similarly nonvented but released at the surface. Descended fish were also over one and a half times more likely to survive than vented fish. Previous studies involving descender devices have proven them beneficial for increasing postrelease survival in several species of Pacific rockfish *Sebastes* sp. (Jarvis and Lowe 2008; Hochhalter and Reed 2011; Rogers et al. 2011; Hannah et al. 2012; Pribyl et al. 2012) and Australian snapper *Lutjanus* sp. (Sumpton et al. 2010; Butcher et al. 2012). The reversal of barotrauma injuries through rapid recompression shows similar benefits for Red Snapper in the Gulf of Mexico. Additionally, the survival of descended fish in our study showed less seasonal variability than with other release treatments. While sea surface temperatures during tagging trials significantly differed by season, water temperatures at the seafloor were stable throughout the year. Returning fish to these cooler water temperatures by using descending devices seems to further enhance postrelease survival and appears to be particularly important when seasonal thermoclines create stratification in the water column.

The severity of barotrauma symptoms increases with capture depth (Alós 2008; Hannah et al. 2008a; Brown et al. 2010; Campbell et al. 2010b; Butcher et al. 2012), and the majority of deepwater catch-and-release studies have identified this variable as the greatest predictor of release mortality.

TABLE 2. Cox proportional hazards model using treatment, season, depth, and total length (TL) as covariates. The hazard ratio shows the proportional risk of each level of a particular treatment against the baseline risk of mortality. For the continuous covariate of total length, the proportional risk is based on a difference of one unit (i.e., 1 mm).

Covariate	Coefficient (b)	SE	Hazard ratio (e^b)	95% CI for e^b	P
Control	baseline				
Descend	0.818	1.010	2.267	0.263–19.574	0.457
Vent	1.311	1.138	3.708	0.399–34.847	0.249
Nonvent	1.927	1.043	6.868	0.889–53.056	0.065
Spring	baseline				
Winter	0.487	0.735	1.627	0.385–6.871	0.508
Summer	1.607	0.683	4.986	1.308–19.013	0.019
30 m	baseline				
50 m	0.925	0.684	2.522	0.660–9.641	0.176
TL	−0.009	0.004	0.991	0.983–0.999	0.039

Results from our study concur with previous findings as fish captured in the shallower (30-m) depth were more likely to survive than those captured at the deeper (50-m) depth. Survival during the spring trials when two depths were compared was 88% at 30 m and 65% at 50 m. Both of these estimates fall within the range of the SEDAR31-DW22 meta-analysis estimates (Campbell et al. 2012) but are nearer the lower boundary. A similar depth influence was documented in Pacific rockfish *Sebastes* spp. (Hannah et al. 2008b), West Australian Dhufish *Glaucosoma hebraicum* (St John and Syers 2005), Painted Comber *Serranus scriba* (Alós 2008), Gag *Mycteroperca microlepis* (Burns et al. 2002; Rudershausen et al. 2007; Sauls 2014), and most pertinently Red Snapper, for which depth was the most important factor in determining release mortality (Campbell et al. 2013).

The apparent correlation between mortality and depth is most likely due to the link between depth and the extent of barotrauma injuries caused by catastrophic decompression (Rummer 2007; Campbell et al. 2010a; Pribyl et al. 2011). The severity of barotrauma symptoms typically increases with depth, as increased pressure causes higher volumetric expansion of internal gases. However, in some studies visible barotrauma symptoms from fish caught in deeper waters appeared reduced or absent (Brown et al. 2010; Campbell et al. 2013). Further examination revealed that this absence of visible barotrauma injuries can occur when the swim bladder ruptures from overexpansion of gases (Rummer 2007; Rogers et al. 2008; Roach et al. 2011; Campbell et al. 2013; Kerwath et al. 2013). This allows internal organs (i.e., stomach or intestines) that would otherwise be displaced to remain inside the body cavity so that the fish may appear healthy and unafflicted by barotrauma injuries upon surfacing when in fact their survival chances are severely depressed. Furthermore, fish with ruptured swim bladders may have neutral or negative buoyancy allowing them to easily resubmerge and presumably survive, when in fact they simply sink to the bottom and perish. Thus, we recommend cautious use of fish condition indices as proxies for predicting postrelease survival in fish suffering from barotrauma as these indices may have a tendency to underreport overall discard mortality because the visible extent of barotrauma symptoms present may not be indicative of the ultimate fate of the fish.

Estimates of Delayed Mortality

A unique aspect in integrating accelerometer and depth sensors into acoustic transmitters was the ability to detect exactly when delayed mortality was occurring. The total mortality estimate of 28% (surface + delayed) is similar to previous estimates of discard mortality found at these depths in SEDAR33 (Campbell et al. 2013), though typically studies from this meta-analysis did not include estimates of delayed mortality. The 11 fish that experienced delayed mortality in our trials persisted for less than 3 d before perishing. At that point in time, acceleration values became 0 and depth reflected the site depth, illustrating that fish were not moving and were likely lying on the seafloor. The transmitters of several fish continued to transmit these data for days to weeks after mortality had occurred. Without acceleration and depth sensor data these fish would in all likelihood have been classified as survivors that exhibited high site fidelity throughout the duration of the transmitter tag life, instead of being classified as fish that perished within 3 d following catch and release. The ability to differentiate mortality from survival is obviously of paramount importance in tagging studies that assess postrelease mortality but also for those estimating site fidelity, residency time, and migration patterns. Acoustic tags that lack sensor data and only relay presence or absence information may be insufficient to answer questions addressing these topics. Based on the

finding of delayed mortality occurring at 3 d, we recommend that any studies assessing postrelease mortality of Red Snapper should monitor fish for a minimum time period of 3 d to ensure that lingering effects of the catch-and-release process that may cause mortality are accurately documented.

This study was able to account for barotrauma-induced delayed mortality in addition to surface mortality through the use of ultrasonic acoustic telemetry. Previous researchers estimating delayed mortality of Red Snapper in the field have relied on caging experiments, which have an inherent bias because they exclude predatory effects, prevent foraging, and restrict natural movement (Campbell et al. 2013). In such studies, separating the influence of caging effects from barotrauma affliction in estimating mortality is difficult. Delayed mortality estimates in caging studies ranged from 20% to 71% at depths from 20 to 50 m (Gitschlag and Renaud 1994; Render and Wilson 1994; Diamond and Campbell 2009). Acoustic telemetry allowed us to estimate delayed mortality in fish that were unrestricted in movement and behavior. Comparatively, we found delayed mortality estimates ranging from 0% to 22%. The estimates of survival in this study were higher than those reported from caging studies, suggesting that the effect of caging itself may be an influential factor that contributes to postrelease mortality. The exclusion of predators should enhance survival, but this is seemingly less important than the need to move unrestricted, presumably to forage. Predator abundance is typically low and highly variable, so the benefits of caging are minimal when compared with the energetic requirements needed to survive. Using acoustic telemetry eliminates one bias associated with caging practices and allows fish to behave unhindered, thus representing a more natural postrelease scenario.

Limitations of Acoustic Telemetry

A primary challenge in using acoustic telemetry for estimating delayed mortality when compared with passive mark–recapture methods is a limitation of sample size. The inherent cost of these transmitters restricts the use of large sample sizes and complex study designs, which are possible to attain using traditional passive tags. Additionally, the risk of tag collisions using this acoustic technology restricted our sample size on an individual site. The use of other acoustic technologies on the market that do not incur tag collision issues may provide a solution to this limitation, and future studies by our research group seek to explore these options. Nonetheless, the tradeoff of low sample size is far outweighed by the fact that investigators can remotely determine the fate of the fish in most cases and do not have to rely on recaptures or the unknowns associated with unrecovered fish. Certainly some disadvantages are associated with the detection limits of acoustic receivers and the variability in detection efficiency because of environmental fluctuation, and these should be accounted for through

rigorous range testing (How and de Lestang 2012; Kessel et al. 2014). However, using reef fish that exhibit high site fidelity, such as Red Snapper (Szedlmayer and Schroepfer 2005; Westmeyer et al. 2007; Topping and Szedlmayer 2011b), increases the likelihood of detection as they typically remain within the range of receivers positioned on the structure.

Many acoustic telemetry studies have noted that a substantial portion of tagged fish have an immediate postrelease emigration event, likely in response to capture and handling stress (Schroepfer and Szedlmayer 2006; Lowe et al. 2009; Topping and Szedlmayer 2011a). This rapid emigration quickly moves fish outside the detection range, with few to zero acoustic transmissions being detected. Without this acoustic information, and if fish are never recaptured, the fate of these emigrants remains unknown. In the present study, 25 of 111 (22.5%) individuals recorded too few acoustic detections to classify fate with any confidence. These fish classified as unknown were omitted from inclusion in the survival analysis, which reduced the experimental sample size. However, the number of unknown fish was fairly consistent across seasons and release treatments, and because of this trend, the omission of the unknowns would not bias one group unfairly with a disproportionate sample size compared with the other groups. Despite the low sample size, several patterns still emerged, and future replication using acoustic tagging would help further support these discard mortality estimates.

Conclusions and Implications

Of central importance to effective fisheries management is the ability to accurately estimate population demographic parameters for stock assessments. For Red Snapper in the Gulf of Mexico, a high level of uncertainty has surrounded estimates of discard mortality, which represents an important parameter due to the high volume of discards that occur in this fishery. Historically, managers have focused on immediate mortality but have not incorporated delayed mortality into population models. If delayed loss is not accounted for in stock assessment models, it is likely that total mortality will be underestimated. Until recently, researchers faced inherent limitations with the methods involved in making these mortality estimates. We have shown that acoustic telemetry possesses the ability to overcome some of these challenges, but results must endure further replication to overcome the inherent low sample sizes before implementation into the stock assessment process.

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